ESTIMATING SIZES OF FISH CONSUMED BY ICE SEALS USING OTOLITH LENGTH – FISH LENGTH RELATIONSHIPS

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Abstract

Arctic fishes and ice seals are key components of the Alaskan Arctic ecosystem. Bearded (*Erignathus barbatus*), spotted (*Phoca largha*) and ringed (*Pusa hispida*) seals are consumers of Arctic marine fishes. Little is known about the sizes of fish that ice seals consume because prey items are digested quickly once exposed to stomach acids. Otoliths, fish ear bones, are often the only parts of a fish that remain in a seal stomach. Otolith length relates directly to fish length, making size estimations of consumed fish possible for piscivore diet studies. Otoliths were measured from fishes collected from cruises in the Beaufort and Chukchi seas during 2009 – 2014. Otolith length – fish length and fish length – fish weight relationships were developed for 11 Arctic marine fish species that are commonly consumed by ice seals in Alaska. Otoliths from seal stomachs provided by subsistence hunters to the Alaska Department of Fish and Game were identified to species level and measured for total length. A mixed effects model was used to determine how the variables of seal species, harvest location, seal age class and sex influenced the sizes of fish consumed. Harvest location and seal age class were the primary factors that affected fish size in ice seal stomachs. Estimating length and weights of fishes consumed by ice seals will help further diet and energetics studies that have not previously been possible in the Alaskan Arctic.

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General Introduction

Arctic fishes provide an essential connection between lower tropic levels (Craig 1984) and sea ice-associated seals, and seals provide major links between humans and the Arctic marine ecosystem (Bluhm and Gradinger 2008). With the Arctic rapidly changing, it is important to understand the current status of important trophic linkages to determine how future ecosystem changes might affect these food webs (Wassmann et al. 2011). Fishes are a major component of seal diets and are likely to be strongly affected by the changing climate. The purpose of this study was to develop otolith length – fish length relationships of fish species commonly present in ice seal diets and to apply these relationships to otoliths found in ice seal stomachs to estimate fish sizes consumed by ice seals.

Four species of seals in Alaska, bearded (*Erignathus barbatus*), spotted (*Phoca largha*), ringed (*Pusa hispida*), and ribbon (*Histriophoca fasciata*) seals are called ice seals because they depend on sea ice for some part of their life history. This study focuses on three of these species; ribbon seals were not included as they are relatively rare, samples are less available, and stomachs are mostly empty (Frost and Lowry 1980). All three seal species prey upon fishes to varying degrees in the Bering, Chukchi and Beaufort seas (Dehn et al. 2007). Bearded seals are mostly benthic feeders, including benthic fish prey such as sculpins and flatfishes, whereas both spotted and ringed seals are mostly pelagic feeders; this results in some prey species differences among these piscivores.

The fish diets of ice seals can be described using fish ear bones, called otoliths. Otoliths are calcified structures that are typically the last part of the fish to be digested and can be passed through the intestinal system minimally digested (Murie and Lavigne 1986). Otoliths have species-specific shapes that allow identification of fishes that have been consumed. Otolith length (OL) is strongly related to fish length (FL), making it possible to estimate length of the fish consumed (Campana 1990). In turn, fish length is strongly related to fish weight (FW) making it also possible to estimate weights of consumed fishes. Developing relationships between OL and FL and FL and FW can aid in developing a better understanding of quantitative diet composition of Arctic piscivores, such as ice seals.

Fish species differ in their energetic values. Fishes with higher energy content are considered nutritionally more beneficial to an ice seal. For example, Capelin (*Mallotus villosus*), Pacific Sand Lance (*Ammodytes hexapterus*), and Arctic Cod (*Boreogadus saida*) have especially high energetic values (Van Pelt et al. 1997, Harter et al. 2013) and may thus be more valuable to an ice seal than species with lower energetic content. At the same time, energy intake by a predator is also determined by prey size, because a larger fish generally has higher total energetic value than a smaller fish. By applying OLFL relationships, the identity and size of fish can be determined; using known energy content of Arctic fishes, it is then possible to determine how much energy fish contribute to ice seal diet.

Multiple factors likely drive the composition and size structure of prey fishes in ice seal diets. On the prey side, one of these factors is that fish size can vary by region. For example, sizes of fish in the Beaufort and Chukchi seas are different from their counterparts in the Bering Sea (Helser et al. 2015). This indicates that OLFL relationships also could differ by region. This regionally specific feature makes it important to examine OLFL relationships for species of interest among study regions, to ensure proper size estimation of fish prey species. In addition, it is possible that OLFL relationships may change in the environment as energy allocation to various body functions such as growth, respiration, reproduction, etc. change with warming water temperatures (Mosegaard et al. 1988). OLFL relationships were developed for some Arctic fishes in the 1970s (Frost and Lowry 1981), but no more recent or regionally-resolved OLFL relationships are available for fish species in the Alaskan Arctic. Given the dramatic changes in the Arctic environment of decreasing sea ice cover and increasing heat budget over the past 40 years (Stroeve et al. 2007, Frey et al. 2015, Wood et al. 2015), the results of this study are especially timely. On the predator side, seal age and location of foraging area are factors that can influence the composition and size structure of an ice seal's fish diet. Seal age determines a seal's ability to dive deeper and longer (Noren et al. 2005). The longer a seal can remain underwater, the larger the opportunity there is to encounter larger numbers of fishes to capture and consume. Foraging location could influence sizes of fishes consumed, if fish sizes or population structures indeed differ among regions.

The goal of this study was to provide a better understanding of ice seals and their fish prey under current conditions in the Arctic. The specific objectives of this study were to 1) provide OLFL and FLFW relationships for 11 fish species in the Chukchi and Beaufort seas, 2) determine sizes of fishes consumed by three common ice seal species in the Alaskan Arctic by applying these relationships to otoliths found in ice seal stomachs, and 3) determine differences in fish prey size among and within seal species by harvest location, age and sex.

Chapter 1

Otolith length – fish length and fish length – fish weight relationships for 11 Pacific Arctic marine fish species

Abstract

Arctic fishes are a key component of the Arctic ecosystem. Determining sizes of fish consumed by marine predators is difficult because otoliths are often the only part of the fish left after digestion. By developing species-specific otolith to body morphometric relationships for Arctic marine fishes, length and weight can be estimated for fish eaten by marine piscivores. Fishes were collected during ice free months in the Beaufort and Chukchi seas during 2009 – 2014, and the most prevalent species captured that were also those most often eaten by ice associated seals were chosen for analysis. Otoliths from 11 fish species from seven families were measured. Strong linear relationships between otolith length and fish total length were observed in all species examined. Coefficient of determination values over 0.80 were recorded for nine of the species examined. All 11 species had very strong fish length – fish weight relationships. The development of otolith length – fish length and fish length – fish weight relationships for key Arctic fish species is an important advance allowing for bioenergetics studies of marine piscivores, providing insight into prey requirements of predators and predator-prey interactions in the Arctic.

Introduction

Fishes are an important part of the Arctic food web (Craig 1984, Bluhm and Gradinger 2008, Eriksen et al. 2012) representing essential connections between upper trophic level predators, such as seals, and lower trophic level species, such as benthic and pelagic invertebrates (Cooper et al. 2009, Majewski et al. 2013). Birds and marine mammals prey on a mixture of demersal and pelagic fishes. There are 45 known families of fishes present in the Pacific Arctic (Mecklenburg et al. 2011). From these 45 families, species such as Capelin (*Mallotus villosus*), Arctic Cod (*Boreogadus saida*), Saffron Cod (*Eleginus gracilis*), sculpins, eelpouts, eelblennies, Pacific Sand Lance (*Ammodytes hexapterus*) and flatfishes are commonly consumed by marine piscivores.

Fish otoliths or ear bones have been used to reconstruct the diets of fish predators. Otoliths are calcium carbonate structures that are more resistant to digestion than soft tissues. Of the three pairs of otoliths found in fishes, the sagittal pair is the most widely used for aging and species identification purposes (Campana and Neilson 1985). Otolith shape varies by species (Harvey et al. 2000). This trait, and their resistance to digestion, makes them useful in identification of consumed prey (Harvey et al. 2000). Otoliths found in scat and stomachs can be identified to species level if they have not been too eroded during digestion. If otolith length and fish length relationships have been established they can also be used to determine sizes of fishes eaten. Otolith length and fish length are strongly correlated (Campana 1990) and this relationship is species-specific (Campana 2005, Harvey et al. 2000). Once a species-specific relationship has been determined, it is possible to estimate fish length using otolith length (Frost and Lowry 1981, Lidster et al. 1994, Ross et al. 2005). Fish weight is also positively related to fish length, making it possible to estimate fish weight when otolith length can be measured (Gamboa 1991, Harvey et al. 2000) although the weight relationship tends to be more variable.

Otolith length – fish length (OLFL) and fish length – fish weight (FLFW) relationships have been used to reconstruct diets of marine mammals (Frost and Lowry 1981), birds (Ross et al. 2005) and even other fish (Jackson et al. 2000). Otolith length – fish weight relationships have been used to estimate biomass of fishes consumed by California sea lions (*Zalophus californianus*) (Gamboa 1991). Several marine mammal – fisheries interactions were studied using OLFL relationships including grey seals (*Halichoerus grypus*) preference for commercial sizes of Silver Hake (*Merluccius bilinearis*) and Atlantic Herring (*Clupea harengus*) (Bowen et al. 1993) and fur seals, sea lions, spotted seals and Walleye Pollock (*Gadus chalcogrammus*) in the Bering Sea (Lowry et al. 1986). OLFL relationships have added to the understanding of diet of several piscivorous whale species such as Baird's beaked whales (*Berardius bairdii*) and beluga whales (*Delphinapterus leucas*) (Walker et al. 2002, Quakenbush et al. 2015). OLFL relationships were used to estimate biomass of fishes consumed by American white pelicans (*Pelecanus erythrorhynchos*) and double crested cormorants (*Phalacrocorax auritus*) on the

North Platte River and Great Lakes region (Derby and Lovvorn 1997, Ross et al. 2005). To determine sizes of forage fishes consumed by Lancetfish (*Alepisaurus ferox*), Swordfish (*Xiphias gladius*) and Yellowfin Tuna (*Thunnus albacores*), OLFL relationships were developed for several species of forage fishes, sardines and myctophid species, in the Indian Ocean (Potier et al. 2007). Salmonid diet studies in Norway used OLFL relationships to determine sizes of sticklebacks consumed by different sizes of adult Arctic Char (*Salvelinus alpinus*) and Brown Trout (*Salmo trutta*) (L'Abée-Lund et al. 1992).

OLFL relationships have been found to vary by region. For example, Red Snapper (*Etelis carbunculus*) OLFL relationships differ among populations in the Pacific Ocean (i.e., Hawaii, Vanuatu, Fiji and French Polynesia; (Smith 1992), as do Haddock (*Melanogrammus aeglefinus*) on Georges Bank and Atlantic Herring in the Atlantic Ocean (Munk et al. 1991, Begg and Brown 2000). Therefore, it is reasonable to expect that the OLFL for Pacific Arctic species may be different among the Bering, Chukchi, and Beaufort seas due to known differences in water temperature and available nutrients (Carmack and Macdonald 2002, Helser et al. 2015). These regional differences reinforce the need to develop OLFL relationships for fish species in the Pacific Arctic to best understand marine predator diet and energetics.

The Chukchi and Beaufort seas compose the Pacific portion of the Arctic Ocean. These two seas have different oceanographic and biological characteristics (Macdonald et al. 1987, Carmack and Macdonald 2002, Crawford et al. 2012). The Chukchi Sea receives high amounts of nutrients from the Bering Sea through Bering Strait and is considered to be more productive than the Beaufort Sea (Macdonald et al. 1987, Carmack and McLaughlin 2011). These differences in productivity suggest a potential for greater growth and size of fishes present in the Chukchi Sea than in the Beaufort Sea.

In this study, I determined OLFL and FLFW relationships for 11 fish important as prey to marine mammals, birds and fish in the Chukchi and Beaufort seas to better understand marine predator diet in the Pacific Arctic.

Methods

Fishes were collected during ice free months (August and September) in the Chukchi and Beaufort seas 2009 – 2014 (Figure 1.1). In the Chukchi Sea, fishes were collected from stations in water 17 – 80 m in depth during 2009–2012. Stations were sampled from the Bering Strait north to latitude 75° N. In the Beaufort Sea, fishes were collected during four research cruises during 2011 – 2014 at on-shelf and off-shelf stations in water depths from 13 to 1,000 m. In 2011, a total of 81 stations were sampled between 155.25 and 145.09° W. Cruises in 2012, 2013 and 2014 sampled a total of 53 stations between longitudes 151.50° W and 137.00° W. These cruises covered the area from Point Barrow to the Mackenzie River Delta in Canada.

Specimens were captured using four types of bottom trawls: 1) the plumb staff beam trawl had 7 mm mesh in the body and 4 mm mesh in the codend, 2) the Canadian beam trawl had a 10 mm mesh in the body and a 6 mm mesh in the codend, 3) the otter trawl had 38 mm mesh in the body and 19 mm mesh in the codend, and 4) the NOAA 83-112 eastern trawl had 102 mm mesh in the body and 32 mm in the codend. Captured fishes were euthanized with MS-222 using a protocol approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC protocol #07-047). Fishes were identified to species level using the methods of Mecklenburg et al. (2002). After identification, fishes were frozen in seawater and shipped to the UAF Fisheries Oceanography Laboratory for further processing.

Eleven fish species were selected for OL vs. FL analysis based on their prevalence in trawl catches and their frequency of occurrence in ice seal stomachs sampled by the Alaska Department of Fish and Game, Arctic Marine Mammal Program: Capelin, Arctic Cod, Saffron Cod, Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*), Shorthorn Sculpin (*Myoxocephalus scorpius*), Canadian Eelpout (*Lycodes polaris*), Stout Eelblenny (*Anisarchus medius*), Slender Eelblenny (*Lumpenus fabricii*), Pacific Sand Lance, Bering Flounder (*Hippoglossoides robustus*) and Yellowfin Sole (*Limanda aspera*). In the lab, all fish were weighed to the nearest 0.01 g and measured for total length to the nearest 1.0 mm. Total length was measured from the tip of the snout to the end of the longest lobe of the caudal fin. A total of 1,396 fish were measured. For each species, 20 fish from each 10 mm size class were randomly selected from the Beaufort Sea samples and from the Chukchi Sea samples, separately, for otolith measurement. Both sagittal otoliths were removed, cleaned, dried and stored in vials. Otoliths were photographed using a Leica DFC295 camera mounted onto a Leica M165C dissecting scope. One otolith from each fish was measured from rostrum to postrostrum to the nearest 0.0001 mm using a Leica imaging software program. The software was calibrated before each session of measurements.

Least squares linear regressions (linear regressions) were used to describe the relationship between OL and FL (Frost and Lowry 1981). Linear regressions were calculated using SigmaPlot Version 12.5 (Systat Software, San Jose, CA). The following linear equation was used to explain the relationship between otolith length and fish length: $y = a + bx$, where y is fish length, a is intercept, b is slope and x is otolith length

To determine if OLFL relationships within a species were different between the Chukchi and Beaufort seas, a least squares linear regression was calculated for each species for both seas and slope and intercept coefficients were compared using a two sample t-test as described by Zar (1999). If the test of slope coefficients were not significant ($\alpha > 0.05$), the intercept coefficients were then tested. If both slope and intercept coefficients were similar, a single linear regression equation was used for the species. If at least one coefficient was significantly different, separate linear regression equations were used for each sea.

Several methods were used to determine if a linear regression provided sufficient estimation precision for use in fish length estimation. Confidence intervals (CI) were used to interpret how close observed data points were to the mean (Montgomery et al. 2012). Prediction intervals identified the expected range of additional (i.e., larger or smaller) observations based on the current data's relationship with the mean. Values of r^2 determined how much variation the linear regression explained. Data points that were greater than or less than three studentized residuals from the mean were considered outliers and omitted from further analysis to further strengthen the relationship. The remaining data were used in all analyses.

Weight – length relationships were also calculated for each species. A power function was used to fit the data and show the curvilinear relationship between FW and FL. Equations were developed for all 11 species using data from all specimens with available weight information (n = 11,057) from the UAF Fisheries Oceanography Laboratory specimen collection, including, but not limited to, the specimens used for developing the OLFL relationships. These specimens were chosen from the same cruises and years to accurately reflect FLFW relationships in those years. The standard fisheries weight regression (Ricker 1975) was used: $W = aL^b$, where W is fish weight, a is intercept, L is fish total length and b is the regression coefficient.

Results

Otolith shape was unique for each species. Capelin otoliths were round with a pronounced rostrum and were always semitransparent (Figure 1.3a). Otoliths of both cod species were elongate in shape (Figures 1.3b, c). Both sculpin species had elongated otoliths with a distinct rostrum (Figures 1.3d, e). Canadian Eelpout (Figure 1.3f) and both eelblennies (Figures 1.3g, h) had smaller, round otoliths. Pacific Sand Lance otoliths were almond shaped with a small rostrum (Figure 1.3i). Flatfish species had circular otoliths that were large for their body size (Figures 1.3j, k). Capelin had the shortest otolith length range (0.562-1.241 mm) and Bering Flounder had the longest (0.292-4.829 mm).

Each species had a unique OLFL and FLFW relationship. For OLFL, nine of the 11 species had r^2 values > 0.85 (Figure 1.4). The other two species, Capelin and Pacific Sand Lance, had lower r^2 values (0.66 and 0.76), potentially due to smaller sample sizes for these species (Table 1.1). However, Bering Flounder and Yellowfin Sole, the two flatfish species, also had small sample sizes but high r^2 values (0.98, Table 1.1). Significant differences in OLFL relationships between Chukchi and Beaufort samples were found for Arctic Staghorn Sculpin ($t = 1.88$, $p = 0.000$), Canadian Eelpout ($t = -2.35$, $p = 0.009$) and Stout Eelblenny ($t = 0.407$, $p = 0.027$). All three species had different slope coefficients, indicating that the relationship between otolith length and fish length was different for these species between the Chukchi and Beaufort seas. Therefore, in Table 1.1, OLFL are displayed separately for these three species for each sea. Linear regressions for all other species were similar among seas so samples were pooled and a single relationship was calculated. FLFW relationships for all 11 species were strongly curvilinear with very high r^2 values (Table 1.2). The r^2 values for FLFW ranged from 0.77

(Capelin) to 0.99 (Arctic Staghorn Sculpin and Yellowfin Sole) (Table 1.2). Capelin and Pacific Sand Lance had the lowest r^2 values (0.77 and 0.92).

Discussion

These newly characterized OLFL relationships for Arctic marine fishes can be used to reconstruct diets of marine piscivores and increase knowledge of Arctic marine ecosystems. These relationships can also be compared to those established for past populations to detect changes over time. If changes are identified in OLFL relationships for the same species, this could indicate different environmental conditions for growth. In addition to being able to determine lengths of fishes consumed by piscivores, relationships developed in this study can be used to estimate fish weight at time of consumption. These OLFL relationships are new for the Alaskan Arctic and will enable investigations of the energetic needs of marine piscivores in the Arctic. A continuation of this study will apply these otolith lengths and body size relationships to otoliths found in ice seal stomachs.

The reliability of this method depends on how well the sizes of the fish sampled represent the fish populations. If the full length range of a species is not represented in the data set used to create the linear regression equation, then estimates of FL at the higher and lower ends of the length range are less accurate (Tarkan et al. 2007). Therefore, it is not recommended to estimate the length of a fish based on an OL that is outside of the range of the sample dataset used to make the linear regression. Most of the fish sampled in this study were less than 400 mm and probably representative of small to medium sized fish for each species. If marine piscivores prey upon fish larger than those used to develop the equations, then OL and FL measurements from larger fish need to be collected, added to the linear regression, and a new regression fit.

Although differences in OLFL relationships can exist between regions thus limiting the use of these relationships to the area of collection (Campana and Casselman 1993), only three of the eleven fish species analyzed in this study showed a difference in OLFL between the Chukchi and Beaufort seas. One possible explanation could be uneven sample sizes between the Chukchi and Beaufort seas; however, that was only true for one of these species, Canadian Eelpout.

Another possible explanation is that the Chukchi Sea is a more productive region for the growth of these two species, though that is unlikely, as more species would have had a difference in their OLFL relationships between the two seas.

Otoliths erode when exposed to digestive acids (Murie and Lavigne 1986, Lidster et al. 1994, Christiansen et al. 2005). In phocid seal stomachs, most otoliths are completely digested ~12 hours after consumption (Murie and Lavigne 1986). Smaller otoliths from Capelin and Pacific Herring (*Clupea pallasii*) will erode much faster than larger Arctic Cod otoliths (Lidster et al. 1994, Christiansen et al. 2005). The OLFL relationships developed in this study used fresh otoliths dissected from fish caught during sampling cruises, therefore the application of these relationships to otoliths that are eroded by digestive acids would underestimate the size (length and weight) of the fish at time of consumption. Any changes to otolith shape can result in underestimation of FL, therefore only relatively fresh otoliths should be used to estimate FL from stomach contents. Otoliths that show intact species-specific characteristics (such as rostrums, post-rostrums and ventral and dorsal ridges) can be used for species identification and length estimation (Harvey et al. 2000).

Environmental factors may influence OLFL relationships (Gauldie and Crampton 2002). In the Arctic, the effects of climate change are occurring at an accelerated rate (Laidre et al. 2015). Rising temperatures and decreasing sea ice cover are likely to affect distributions of fishes in the coming years (Logerwell et al. 2015). Warmer water temperature could modify OLFL relationships by affecting fish and otolith growth rates. For example, OL at a given FW was shorter for faster growing Arctic Char in warmer waters than for slower growing Arctic Char in colder waters (Mosegaard et al. 1988). Sea ice cover is closely related to food availability for all trophic levels (Springer and McRoy 1993, Grebmeier et al. 2006, Bluhm and Gradinger 2008). Decreasing sea ice cover could influence seasonal nutrient availability and the exchange of nutrients between the benthic and pelagic food webs (Grebmeier et al. 2006). In turn, this could change growth rates of fishes, changing the relationship between OLFL (Gauldie and Nelson 1990, Wright et al. 1990). Therefore, as climate change continues in the Pacific Arctic, established OLFL relationships are expected to change.

The OLFL and FLFW relationships developed in this study can be used to estimate the size, weight, and thus energetic value of fishes. Applying these relationships to fishes consumed by marine piscivores in Alaska will allow diet and energetics studies that have not previously been possible.

Figures

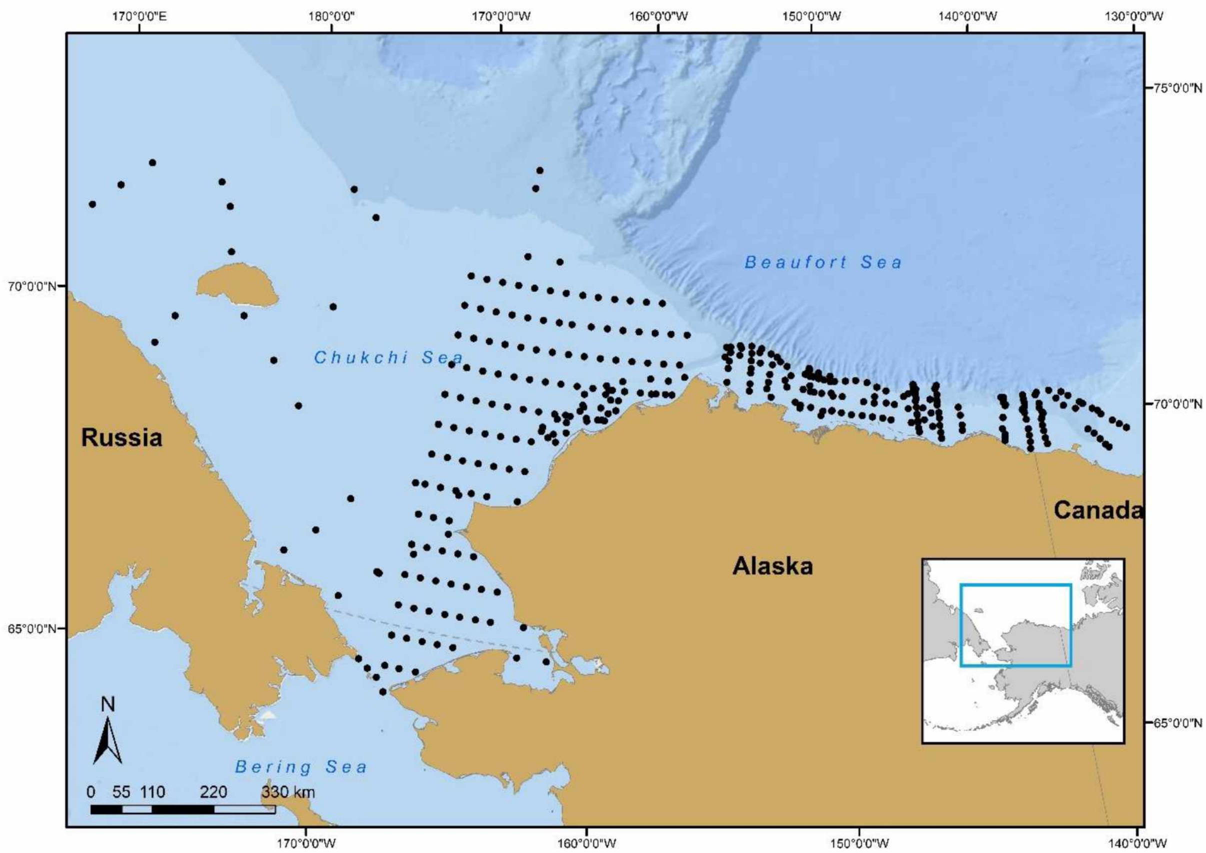

Figure 1.1. Study area with fish sample locations (black dots) during eight research cruises, 2009 – 2014.

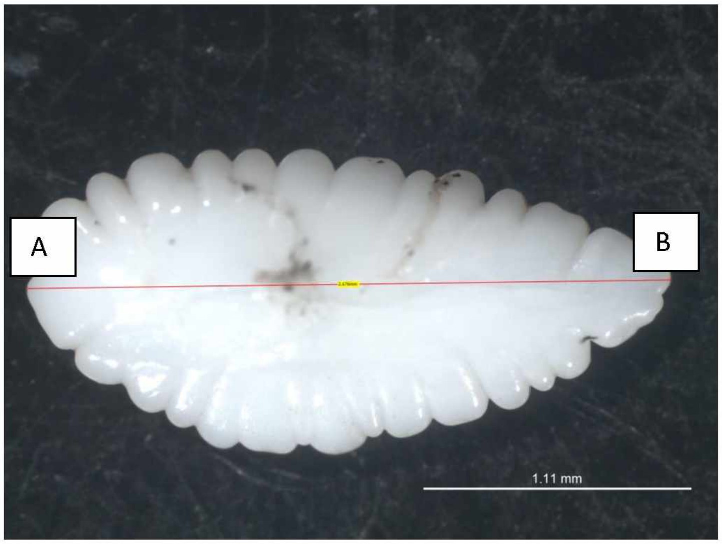

Figure 1.2. Arctic Cod otolith. Red line indicates where length was measured from the rostrum (A) to the postrostrum (B).

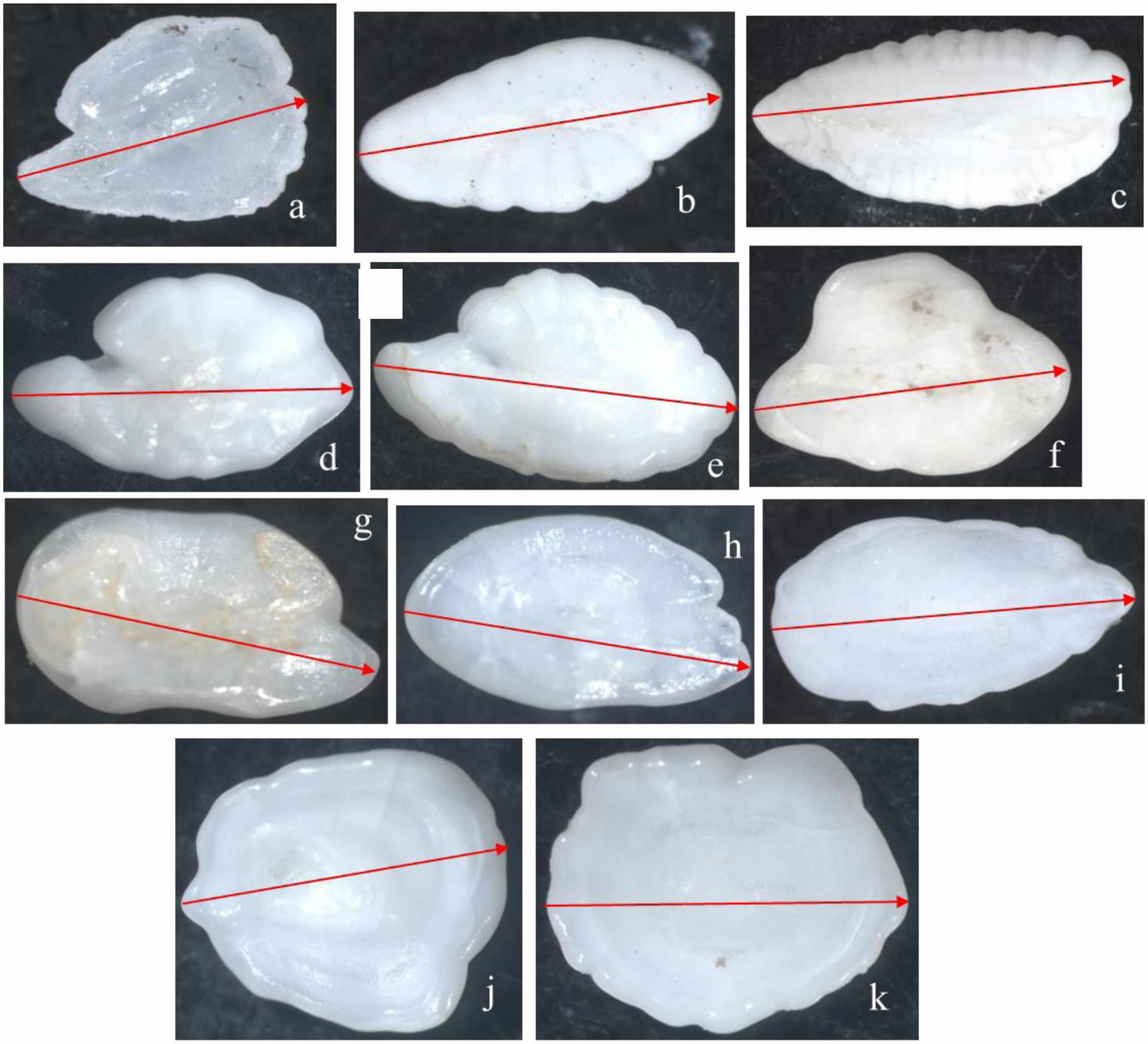

Figure 1.3. Sagittal otoliths from each species with red line designating where lengths were measured. a: Capelin, b: Arctic Cod, c: Saffron Cod, d: Arctic Staghorn Sculpin, e: Shorthorn Sculpin, f: Canadian Eelpout, g: Stout Eelblenny, h: Slender Eelblenny, i: Pacific Sand Lance, j: Bering Flounder, k: Yellowfin Sole

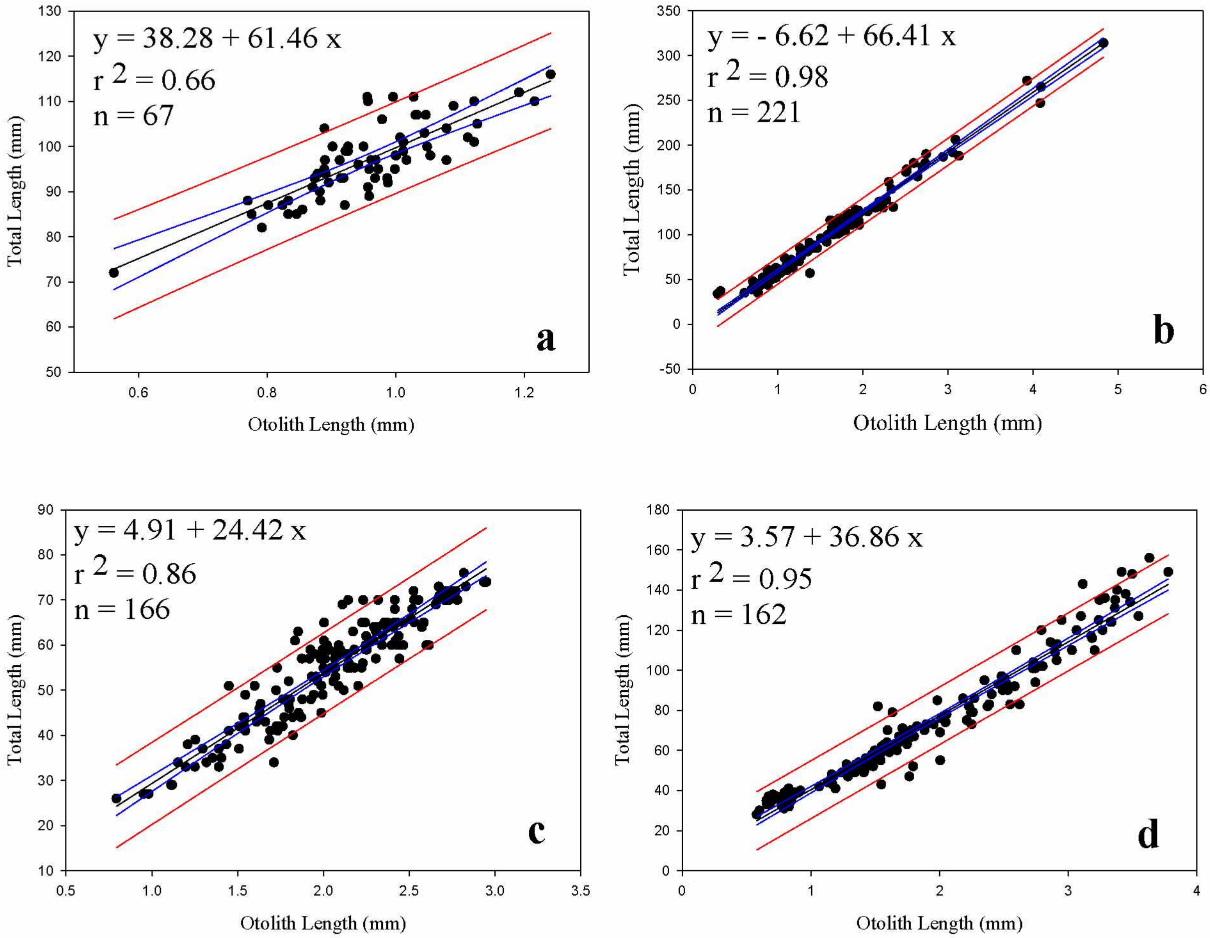

Figure 1.4. OLFL relationships for 11 fish species with linear regression equation, coefficient of determination (r^2) and sample size (n). Blue lines are confidence intervals and red lines are prediction intervals, both 95%. a: Capelin, b: Arctic Cod, c: Saffron Cod, d: Arctic Staghorn Sculpin, e: Shorthorn Sculpin, f: Canadian Eelpout, g: Stout Eelblenny, h: Slender Eelblenny, i: Pacific Sand Lance, j: Bering Flounder, k: Yellowfin Sole

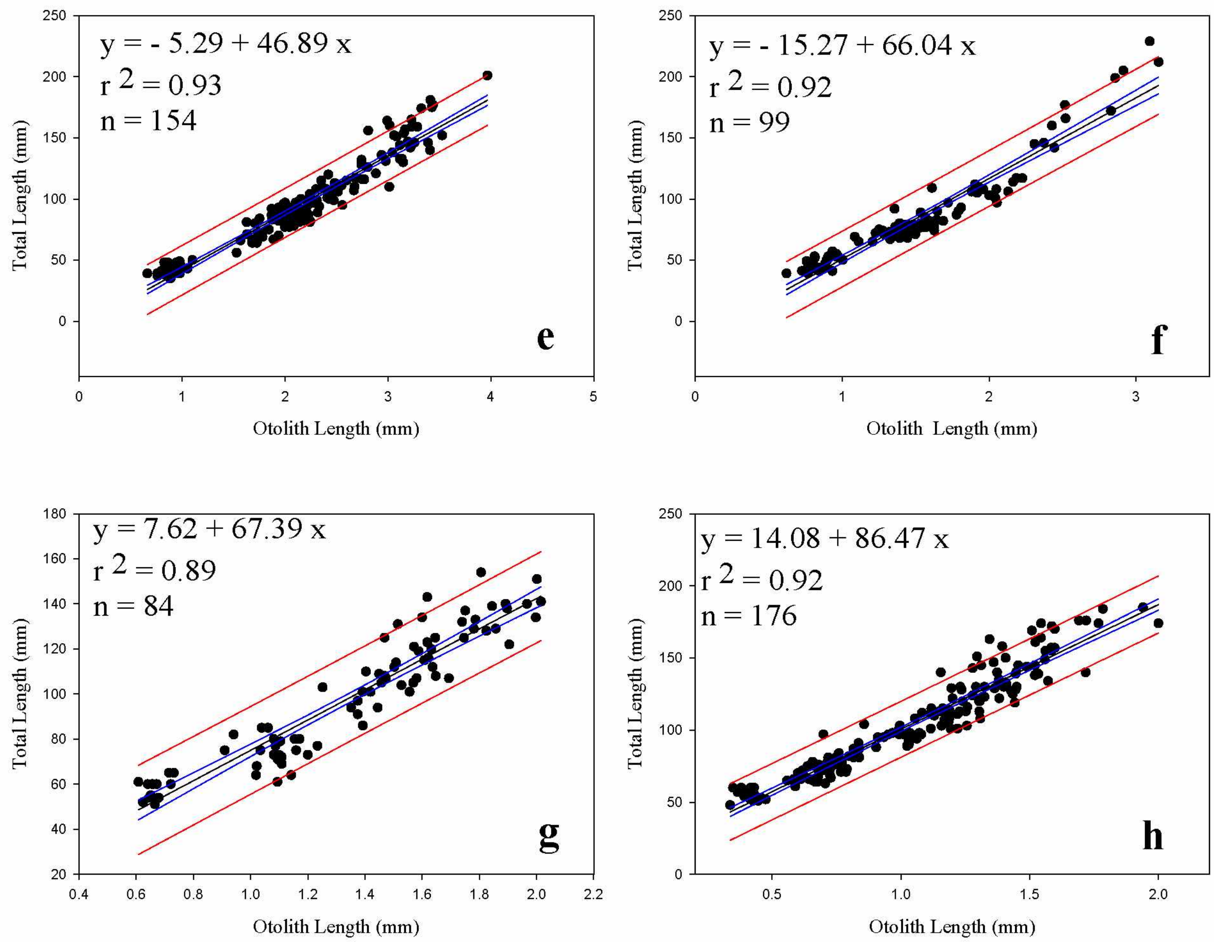

Figure 1.4 continued. OLFL relationships for 11 fish species

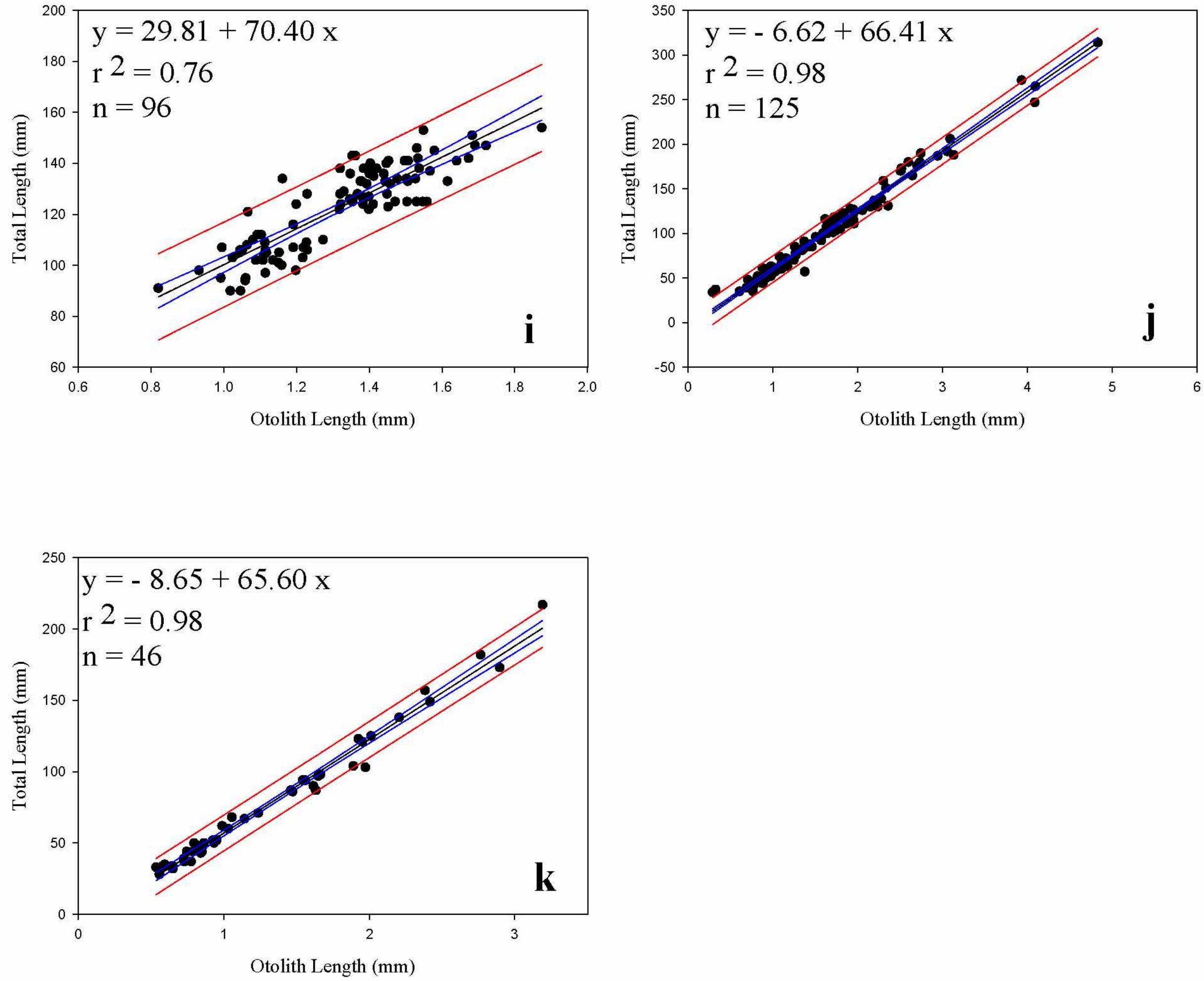

Figure 1.4 continued. OLFL relationships for 11 fish species

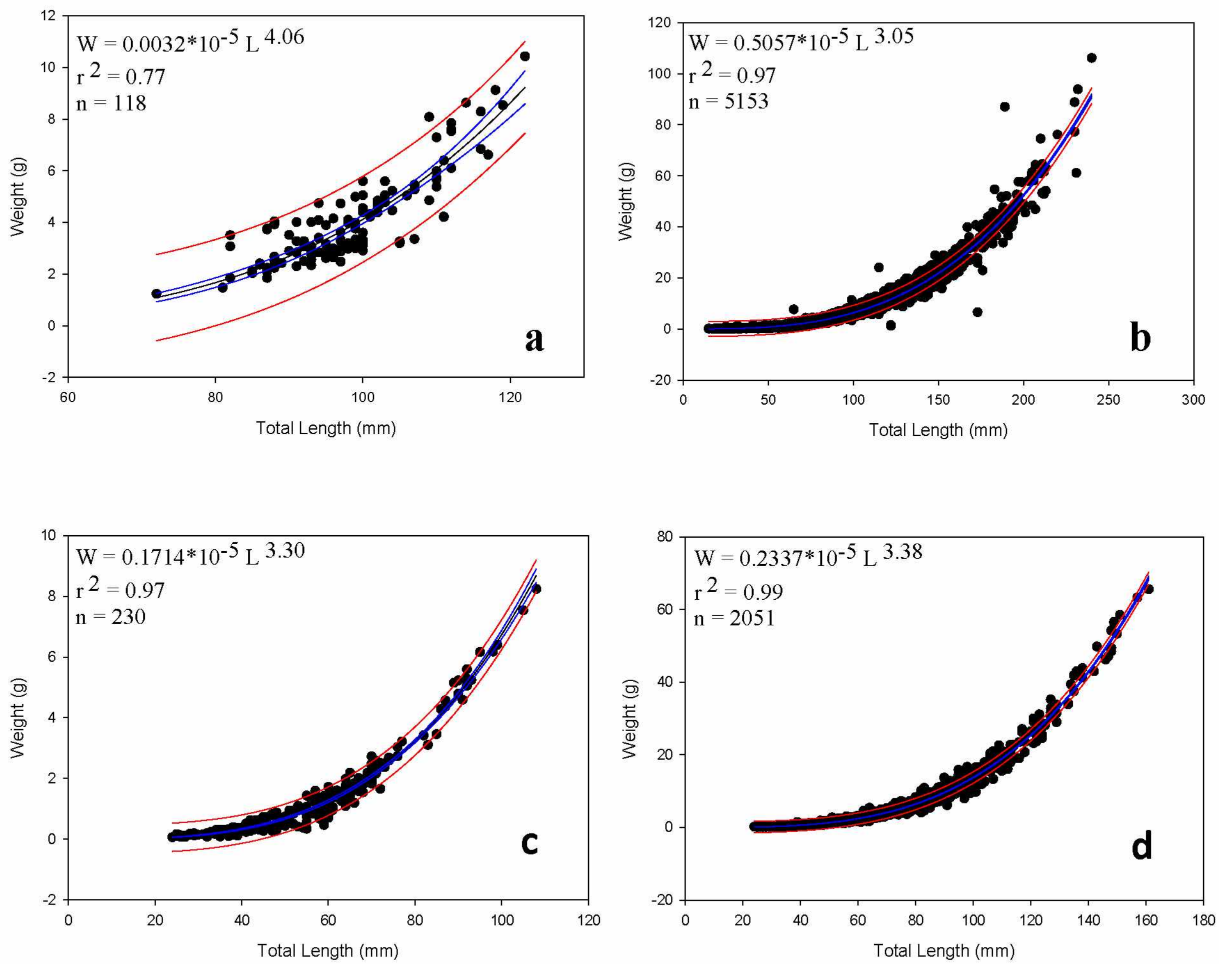

Figure 1.5. FLFW relationships for 11 fish species with linear regression equation, coefficient of determination (r^2) and sample size (n). Blue lines are confidence intervals and red lines indicate prediction intervals, both 95%. a: Capelin, b: Arctic Cod, c: Saffron Cod, d: Arctic Staghorn Sculpin, e: Shorthorn Sculpin, f: Canadian Eelpout, g: Stout Eelblenny, h: Slender Eelblenny, i: Pacific Sand Lance, j: Bering Flounder, k: Yellowfin Sole

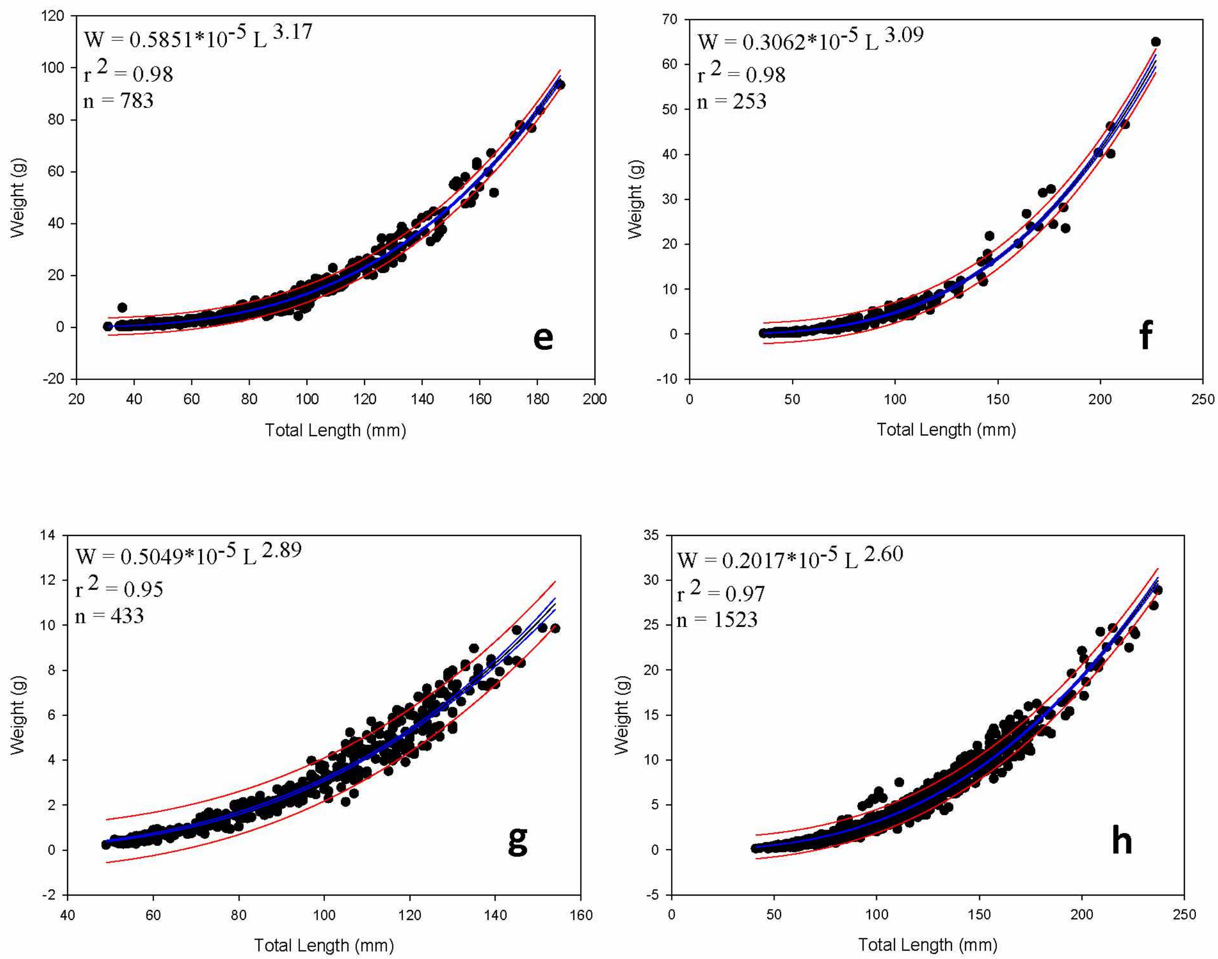

Figure 1.5 continued. FLFW relationships for 11 fish species

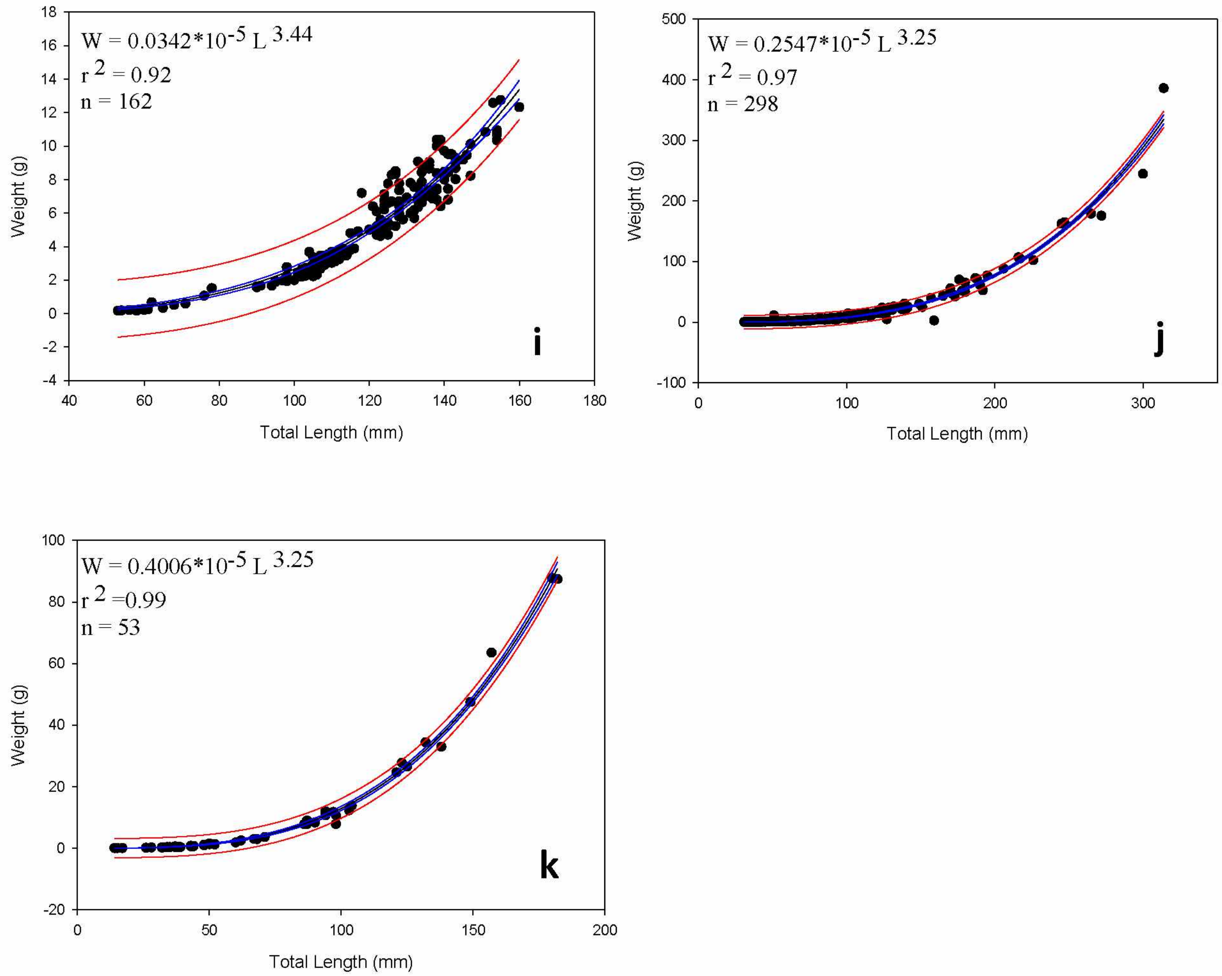

Figure 1.5 continued. FLFW relationships for 11 fish species

Tables

Table 1.1. OLFL relationships for 11 fish species from the Chukchi and Beaufort seas where n is number of fish measured for each species. Fish length is the total length for each species in mm and “min” and “max” provide the range of lengths used to form the relationship equations, “a” is slope, “b” is intercept and r^2 is the coefficient of determination.

Species	n	min	max	a	b	r^2
Osmeridae						
Mallotus villosus	67	72	116	38.28	61.46	0.66
Gadidae						
Boreogadus saida	221	26	158	-6.62	66.41	0.98
Eleginus gracilis	166	33	76	4.91	24.42	0.86
Cottidae						
Gymnocanthus tricuspis						
Chukchi Sea	111	28	156	3.23	37.35	0.96
Beaufort Sea	51	31	101	11.49	30.13	0.85
Myoxocephalus scorpius	154	35	223	-5.29	46.89	0.93
Zoarcidae						
Lycodes polaris						
Chukchi Sea	7	41	229	-28.50	78.44	0.98
Beaufort Sea	92	39	205	-7.47	2.02	0.91
Stichaeidae						
Anisarchus medius						
Chukchi Sea	41	55	154	18.30	63.62	0.94
Beaufort Sea	43	51	134	2.42	67.47	0.84
Lumpenus fabricii	176	48	204	14.08	86.47	0.92
Ammodytidae						
Ammodytes hexapterus	96	90	155	29.81	70.40	0.76
Pleuronectidae						
Hippoglossoides robustus	125	34	314	-6.62	66.41	0.98
Limanda aspera	46	28	217	-8.65	65.60	0.98

Table 1.2. FLFW relationships for 11 fish species from the Chukchi and Beaufort seas combined where n is number of specimens used for analysis. Fish weight is in g and "min" and "max" provide the range of weights used to form the relationship equations, "a" denotes intercept, "b" denotes regression coefficient, and r^2 is the coefficient of determination.

Species	n	min	max	$a * 10^{-5}$	b	r^2
Osmeridae						
Mallotus villosus	118	1.23	10.43	0.0032	4.06	0.77
Gadidae						
Boreogadus saida	5153	0.03	106.1	0.5057	3.05	0.97
Eleginus gracilis	230	0.06	8.24	0.1714	3.30	0.97
Cottidae						
Gymnocanthus tricuspis	2051	0.11	65.6	0.2337	3.38	0.99
Myoxocephalus scorpius	783	0.22	93.42	0.5851	3.17	0.98
Zoarcidae						
Lycodes polaris	253	0.16	65.01	0.3062	3.09	0.98
Sticheaidae						
Anisarchus medius	433	0.23	9.88	0.5049	2.89	0.95
Lumpenus fabricii	1523	0.13	28.88	0.2017	2.60	0.97
Ammodytidae						
Ammodytes hexapterus	162	0.16	12.76	0.0342	3.44	0.92
Pleuronectidae						
Hippoglossoides robustus	298	0.16	386	0.2547	3.25	0.97
Limanda aspera	53	0.03	65.01	0.4006	3.25	0.99

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Chapter 2

Sizes of fish consumed by three species of ice seals in the Alaskan Arctic

Abstract

Alaskan Arctic seals (Family Phocidae), often referred to as "ice seals", are consumers of fish and invertebrates. A large component of the diet of bearded (*Erignathus barbatus*), spotted (*Phoca largha*) and ringed (*Pusa hispida*) seals is fish. Fish otoliths are resistant to digestion and are commonly used to identify fish species during seal stomach content analysis. Although much is known about what fish species are eaten by these ice seals, less is known about the sizes of fish that are eaten. Recently described otolith length – fish length and fish length – fish weight relationships for Arctic fish species were used here to estimate sizes of fish found in stomachs of subsistence-harvested bearded, spotted, and ringed seals in Alaska based on otoliths. The influence of age class (pup, subadult, and adult), sex, harvest location (Utqiagvik (formerly Barrow), Wainwright, Point Hope, Kotzebue, Shishmaref, Little Diomede, and Nome), and seal species on the sizes of fish consumed was investigated. For bearded seals, harvest location was the primary factor influencing sizes of fish consumed. Stomachs from bearded seals harvested near Little Diomede (Bering Strait) contained larger otoliths (i.e., larger fish) of Arctic Cod, Arctic Staghorn Sculpin, and Shorthorn Sculpin than those harvested near Utqiagvik (in the northern Chukchi Sea). Spotted seals harvested near Shishmaref (southern Chukchi Sea) consumed larger Arctic Cod than those harvested near Little Diomede. Adult ringed seals consumed larger Saffron Cod than pups. Estimating the length and weight of fish consumed by ice seals will contribute to studies of diet and energetics that have not been possible previously in the Alaskan Arctic and will aide in understanding changes that may occur as climate change increases water temperatures, decreases sea ice cover, and potentially alters fish distributions.

Introduction

Seals from the family Phocidae that use sea ice as a pupping, resting and feeding platform are called “ice seals”. Three ice seal species are common in the Alaskan Arctic: bearded (*Erignathus barbatus*), spotted (*Phoca largha*), and ringed (*Pusa hispida*) seals. Ice seals are ecologically important as major consumers of fish and invertebrates (Dehn et al. 2007), and are relied upon for subsistence by Native coastal communities in western and northern Alaska (Moore and Huntington 2008).

Ice seals vary by size and diet composition. Bearded seals are the largest ice-associated seal in Alaskan Arctic waters, with adults reaching lengths of up to 2.4 m and weights up to 360 kg (Lowry et al. 1980a). Spotted seals are medium-sized seals up to 1.7 m in length and weights up to 110 kg (Boveng et al. 2009). Lastly, ringed seals are the smallest ice seal with lengths of 1.5 m and weights of up to 75 kg (Lowry et al. 1980b, Kelly et al. 2010). Bearded seals are benthic feeders of fish and invertebrates (Lowry et al. 1980a, Hjelset et al. 1999). Pups typically have a diet of mostly gastropods and bivalves (Crawford et al. 2015) while adult bearded seals consume more fish, mostly sculpins, Arctic Cod (*Boreogadus saida*), flatfish, and pricklebacks (Dehn et al. 2007, Crawford et al. 2015). Spotted seals are primarily pelagic feeders though they are known to prey on some demersal fishes and invertebrates (Dehn et al. 2007). Spotted seals consume mostly Saffron Cod (*Eleginus gracilis*), Arctic Cod, Pacific Herring (*Clupea pallasii*), and Rainbow Smelt (*Osmerus mordax*) (Quakenbush et al. 2009). Ringed seals are also primarily pelagic feeders of fishes and invertebrates (Holst et al. 2001, Dehn et al. 2007), mostly Arctic Cod, Pacific Herring, Rainbow Smelt, and Walleye Pollock (*Gadus chalcogrammus*) (Crawford et al. 2015).

Otoliths, fish ear bones, are somewhat resistant to digestion and can be used to identify prey fish species by inspection of stomach contents. Otolith shape is species specific (Harvey et al. 2000), allowing for fish species identification after consumption. Otolith length and fish length show a positive relationship, allowing estimation of fish length at time of consumption from otoliths found in stomachs. Fish length can also be used to estimate fish weight (Gamboa et al. 1991, Harvey et al. 2000). Otolith length – fish body size relationships have been used to describe fish prey in other fish species, birds, whales, and seals (Frost and Lowry 1981, Ross et al. 2005, Potier et al. 2007, Quakenbush et al. 2015). Recently, relationships for 11 fish species consumed by ice seals have been estimated using fishes collected by the UAF Fisheries Oceanography Laboratory (Chapter 1).

Regional differences in size may occur in fishes commonly consumed by ice seals. For example, Arctic Cod, a common ice seal prey item (Crawford et al. 2015), are larger in the northern Bering Sea relative to conspecifics farther north in the Chukchi Sea, likely due to the warmer temperatures nearshore waters and increased availability of nutrients (Helser et al. 2015). Sizes of fish in ice seal diets could change in the future due to physiological stresses on fishes, which could shift seal distributions as a response to fish prey size in a changing environment (Laidre et al. 2008). By using otolith length to fish length relationships to estimate sizes of fish seals are consuming, it is possible to assess regional size variability of fish in ice seal diets. Information on fish size and energy content are essential components of diet and energetics studies.

Energy content is known to vary by species and size of fish. Pacific Sand Lance (*Ammodytes hexapterus*), Arctic Cod, Saffron Cod, and Capelin (*Mallotus villosus*) are especially energy rich (Van Pelt et al. 1997, Harter et al. 2013, Hop and Gjøsæter 2013), making them potentially valuable forage species for ice seals in the Alaskan Arctic. In addition to being energy rich, Arctic Cod is the most abundant forage fish in the Arctic and is considered a key link between trophic levels (Lowry and Frost 1981, Craig 1984, Hop and Gjøsæter 2013, Helser et al. 2015).

The quantity, quality, and diversity of forage fish consumed by ice seals is not only determined by the available fish species and, in turn, sizes of available fish but also by the age of the seal. Older seals are more experienced foragers and are physiologically able to dive deeper and longer than pups, enabling them to capture more, and potentially larger, fish (Noren et al. 2005). For example, adult ringed seal consume more Arctic Cod than pups (Dehn et al. 2007), and bearded seal adults contain more fish in their diets than do pups (Crawford et al. 2015). Less is known about the sizes of fish eaten by adult seals and pups, which affects the energy intake per foraging effort of these two age classes.

Ice seal diet is likely to be influenced by the changing climate in the Alaskan Arctic. The decrease of sea ice cover in the Arctic and subsequent increase of water temperature has the potential to affect distribution, abundance, and size of important prey for seals (Bluhm and Gradinger 2008, Grebmeier et al. 2010). If changes in prey result in less energy available to seals, seal behavior and distribution will likely change to maintain their energy needs for survival and reproduction (Kovacs et al. 2011). Such ecological consequences of changes in the Arctic increase the urgency for a better understanding of ice seal energy requirements.

The objectives of this study were to 1) determine the sizes of fish consumed by three common ice seals species (bearded, spotted, and ringed seals) in the Alaskan Arctic by applying otolith size to fish size relationships (Chapter 1) to otoliths found in ice seal stomachs, and 2) determine differences in fish prey size among and within seal species by harvest location, age, and sex. Results will support future studies on the energetic value of fishes to ice seals and detect changes in fish size in ice seal diets relative to climate change.

Methods

Ice seals in the Chukchi and Beaufort seas in the Alaskan Arctic are legally harvested by subsistence hunters. Most of the harvest occurs in spring (April, May and June) and fall (September, October, November). Native Alaskan subsistence hunters work with the Alaska Department of Fish and Game, Arctic Marine Mammal Program (ADF&G) to provide samples, including stomachs, from harvested ice seals. This long-term biomonitoring program has an extensive archive of ice seal stomach content data and hard parts (including fish otoliths) that were available for this study.

Seal stomachs were available from villages bordering the Beaufort, Chukchi and Bering seas (Utqiagvik, Wainwright, Point Hope, Kotzebue, Shishmaref, Little Diomede, and Nome; Figure 2.1). This study only included seals whose stomachs contained fish. A stomach was chosen for analysis if it contained more than 10 individual fish from any of the 11 fish species for which otolith length – fish length (OLFL) and fish length – fish weight (FLFW) relationships have been established (Chapter 1). These fish species were Capelin, Arctic Cod, Saffron Cod, Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*), Shorthorn Sculpin (*Myoxocephalus scorpius*), Canadian Eelpout (*Lycodes polaris*), Slender Eelblenny (*Lumpenus fabricii*), Stout Eelblenny (*Anisarchus medius*), Pacific Sand Lance, Bering Flounder (*Hippoglossoides robustus*), and Yellowfin Sole (*Limanda aspera*).

Otoliths were removed after stomach contents were rinsed over a 1.0 mm sieve (Crawford et al. 2015). Otoliths were identified to lowest taxonomic level, usually to species, by William Walker (private contractor with ADF&G). Otoliths from each sample were separated by species, and then right and left otoliths were separated and counted to determine the minimum number of individual fish present in that stomach. Using only right or left otoliths ensured only one measurement per fish, as OLFL relationships generally do not differ between right and left otoliths (Harvey et al. 2000). The exception to this generalization are right-eyed flatfishes, where the left otolith can be somewhat larger than the right otolith (Lychakov et al. 2008). However, when OLFL relationships were described for Bering Flounder and Yellowfin Sole in this study, no difference was detected between the right and left otolith. The otolith (right or left side) to be photographed and measured was determined by the side that was most abundant in each stomach. Otolith lengths were measured using a Leica DFC295 camera mounted on a Leica M165C dissecting scope. Before each photographing session, the camera was calibrated to 0.0001 mm using a slide micrometer. Each otolith length was then measured from the photographs to the nearest 0.0001 mm using a Leica imaging software program.

Fish lengths were estimated from otoliths found in ice seal stomachs using linear equations previously estimated for each of the 11 species listed above using fishes collected during sampling surveys in the Chukchi and Beaufort seas (Chapter 1). Due to regional variability in the OLFL and FLFW relationships between the Chukchi and Beaufort seas for three fish species, Arctic Staghorn Sculpin, Stout Eelblenny and Canadian Eelpout, fish lengths for these three fish species were estimated using the relationship from the Chukchi Sea. Otoliths of fish caught during research surveys and used to establish OLFL and FLFW relationships were often smaller than those found in seal stomachs. Therefore, estimation of fish length of seal prey was restricted to the range of otolith lengths used to produce each linear regression for that fish species (Chapter 1). However, when otoliths found in seal stomachs were larger than those used to establish the OLFL and FLFW relationships, valid comparisons of relative fish size could still be made by using otolith length directly because larger fish within the same species have larger otoliths (Harvey et al. 2000). For this study, a general linear relationship is assumed for each species (Harvey et al. 2000). Therefore, differences in sizes of fish eaten by age class, sex, harvest location, and seal species can be determined using otolith length directly and in this way, all otoliths from seal stomachs could be included.

A linear mixed effects model was used to compare mean otolith length found in seal stomachs. This method was chosen because of the nested nature (i.e. multiple individuals of several different fish species consumed by individual seals) of the data set and to account for the variability within each seal sample. Age class, sex, harvest location and seal species were factors considered to be fixed effects, and individual seals were the random effect. An ANOVA determined if the effects of seals species, harvest location, age class (pup, subadult, adult) or sex significantly affected mean otolith length for each seal species for each fish species. A full model of:

Otolith Length ~ Age class + Sex + Location + Seal Species + (1|Seal)

was used for each fish species consumed by seals, where 1|Seal indicates the random effect of the individual seal and Otolith Length ~ indicates average otolith length. When a factor did not have a significant effect on mean otolith length of that fish species, that factor was removed from the model. Interactions between and among factors were also analyzed to determine if two factors were jointly affecting mean otolith length in a seal stomach. All analyses were completed in R version 3.2.4 using the lme4 (Bates et al. 2015) and lmerTest packages (Kuznetsova et al. 2016).

Results

Among seal species comparisons

A total of 1,867 otoliths from 128 bearded seal stomachs, 1,411 otoliths from 82 spotted seals, and 2,435 otoliths from 145 ringed seals were measured. Roughly 77% of the otoliths in seal stomachs were larger than the range of otolith lengths used to create the OLFL relationships from the results of Chapter 1 and were not used to estimate fish length in this study (Figure 2.4). Many otoliths from Capelin, Arctic Cod, Saffron Cod, Arctic Staghorn Sculpin, Shorthorn Sculpin, Slender Eelblenny, Canadian Eelpout, Pacific Sand Lance, Bering Flounder and Yellowfin Sole consumed by ice seals were larger in length than otoliths used to create the OLFL relationships. Overall, fishes eaten by seals had otoliths that averaged 0.78 mm longer. Maximum otolith lengths used to create the OLFL relationships ranged from 2.18 to 10.45 mm among these ten fish species. All Saffron Cod and Canadian Eelpout consumed by ice seals had otolith lengths larger than those used to establish the OLFL relationships (Figure 2.4) and those lengths could not be used to estimate sizes of fish found in stomachs. Saffron Cod consumed by ice seals had otoliths that averaged 4.96 mm longer than those used to create the original OLFL. For Canadian Eelpout, otolith lengths were 2.25 mm longer in fish eaten by seals. Stout Eelblenny was the only species where average otolith lengths of fish eaten by seals were similar to those used to create the OLFL relationships.

Saffron Cod, Arctic Cod, Capelin, and Pacific Sand Lance were consumed by all three ice seal species ($n = 86$ bearded seals, $n = 81$ spotted seals, and $n = 145$ ringed seals). All three seal species also ate Saffron Cod larger than fish specimens caught during research cruises used to develop OLFL relationships (Chapter 1). Because the Saffron Cod consumed were too large to use in the OLFL equations, a direct comparison of otolith lengths was used and showed that spotted seals consumed the largest Saffron Cod among seal species (mean = 7.96 mm, SD = ± 2.95, $p < 0.001$, $n = 56$ spotted seals, $n = 656$ Saffron Cod), followed by ringed seals (mean = 6.42 mm, SD ± 1.76, $p < 0.001$, $n = 70$ ringed seals, $n = 870$ Saffron Cod), and then bearded seals (mean = 5.27 mm, SD ± 2.19, $p < 0.001$, $n = 37$ bearded seals, $n = 143$ Saffron Cod). In contrast, no differences were found in average otolith lengths for Capelin or Pacific Sand Lance among the three seal species. Spotted seals consumed the largest Arctic Cod (242 mm and

116.18 g, Table 2.1), bearded ate the second largest (229 mm and 85.14 g), followed by ringed seals (214 mm and 73.05 g).

Within seal species comparisons

Average otolith sizes of fish consumed within each of the three seal species were compared by harvest location, seal age class and sex. For bearded seals, only harvest location was significant in the average otolith lengths of fish consumed (Table 2.2); otoliths of Arctic Cod, Arctic Staghorn Sculpin and Shorthorn Sculpin from bearded seals harvested near Little Diomede were significantly larger than those harvested near Utqiagvik, Point Hope, and Shishmaref ($p < 0.001$, Figure 2.3). Based on otoliths found in bearded seal stomachs, fish lengths could be estimated for nine of 11 fish species commonly eaten. Mean estimated fish lengths ranged from 108–163 mm (Table 2.1, Figure 2.2); with Arctic Cod being the longest. Mean fish weights ranged from 4.28–85.14 g; with Arctic Cod weighing the most (Table 2.1). Bering Flounder (mean weight: 36.12 g) and Yellowfin Sole (mean weight: 54.77 g), both flatfishes, were next and the smallest species of fish consumed was Stout Eelblenny at an average 4.28 g.

For spotted seals, harvest location was also the only significant factor influencing fish size (Table 2.2). Arctic Cod found in spotted seals harvested near Shishmaref were larger than those harvested near Little Diomede ($p < 0.001$). Mean fish lengths for seven of eight species consumed by spotted seals ranged from 113–220 mm (Table 2.1, Figure 2.2). Again, otoliths of Saffron Cod were larger than the size range used to develop the relationships. Mean fish weights ranged from 7.08–116.24 g with Shorthorn Sculpin being the heaviest fish species consumed by spotted seals (Table 2.1).

For ringed seals, harvest location and seal age class were significant factors that influenced sizes of fish consumed, but only for Arctic Cod (Table 2.2). Ringed seals harvested near Shishmaref consumed larger fishes than ringed seals harvest near Little Diomede ($p = 0.05$). Adult ringed seals consumed Arctic Cod with larger otoliths than pups ($p = 0.05$). For ringed seals, fish lengths could be estimated for three of seven fish species consumed (mean lengths included Arctic Cod: 214 mm, Shorthorn Sculpin: 158 mm, and Yellowfin Sole: 176 mm, Table

2.1, Figure 2.2). The other four fish species consumed by ringed seals (Capelin, Saffron Cod, Arctic Staghorn Sculpin, and Pacific Sand Lance) had otoliths that were larger than those used to develop the OLFL relationships. Mean fish weights ranged from 54.24 – 79.28 g. Yellowfin Sole weighed the most (79.28 g, Table 2.1) followed by Arctic Cod at 73.05 g.

Discussion

The relationships used to estimate fish length from otolith length did not cover the full range of otoliths found in seal stomachs. Most otolith length – fish size relationships, however, are known to be linear (e.g., Harvey et al. 2000) although they may have inflection points where the relationship changes (Frost and Lowry 1981, Francis 1990). Although an inflection may change the slope of the relationship, it does not change the general relationship that larger otoliths equate to larger fish and smaller otoliths to smaller fish. Therefore, while it was not possible to accurately estimate fish length for large otoliths found in seal stomachs, the assumption that relative otolith length relates to relative fish size is likely valid and can be used for general fish size comparisons using otolith lengths.

To make OLFL relationships more applicable to ice seal diet studies, larger fish need to be added to the dataset used to calculate the relationships for all fish species consumed by ice seals. Identifying fish species and estimating fish length from otolith length are useful tools for studying piscivore diets from stomach contents. Species identification is dependent upon the shape and integrity of species-specific features found on the otolith, such as ridges, scallops and various other identifying features (Campana 1990). Estimating fish lengths accurately is dependent on using otoliths that are not too eroded by digestion (Murie and Lavigne 1986). By using otoliths minimally affected by digestion, this method can be used to study fish prey species composition and size of fish prey in ice seals or other predators (Frost and Lowry 1981).

Fish size (analyzed as otolith size) was significantly related to harvest location for all three seal species. Spotted and bearded seals harvested near Shishmaref and Little Diomede consumed larger fishes (i.e., Arctic Cod, Arctic Staghorn Sculpin, and Shorthorn Sculpin) than those harvested near Utqiagvik or Point Hope (Fig. 2.3). These results suggest either that some fish species are larger in the southern than northern Chukchi Sea or that seals in the southern Chukchi Sea select larger fishes. Regional differences in size distribution are known for these Arctic fish species (Gray et al. 2016, Helser et al. 2015). While harvest location is not necessarily equivalent to foraging location (e.g., phocid seals typically have a foraging range of up to 30 km in a 24 hr period; Lowry et al. 1998, Thompson et al. 1998, Quakenbush et al. 2011, Crawford et al. 2015), the short time that fish otoliths remain in a seal stomach (12-24 hours; Muring and Lavigne 1986, Lidster et al. 1994) suggests that foraging and harvesting locations are reasonably close. This indicates that seals could be valuable biosamplers of regional fish populations and otoliths in their stomachs could provide useful information about regional differences in fish size.

Adult ringed seals ate larger Arctic Cod than pups. This could occur if adult seals have more experience foraging, larger body size, and better diving capabilities (Noren et al. 2005), and prefer or encounter larger fish. Indeed, diving capability increases with age in phocid seals as oxygen storage capacity increases in blood and muscles (Lydersen et al. 1994, Noren et al. 2005). Such ontogenetic patterns are known from Arctic grey seals (*Halichoerus grypus*) where large (adult) individuals consume larger prey than smaller grey seals (Tucker et al. 2007). Older and larger gadids are known to inhabit deeper waters (Laurel et al. 2009) and would, thus, have a higher chance to be encountered by adult seals. While different size selection of forage fish in adults versus pups may be driven by physiological capacities and constraints, the ecological consequence from such spatial (feeding depth) separation is an example of effective resource partitioning among seal age classes, which may reduce intra-specific competition for resources (Field et al. 2005). Although bearded seals also are known to increase diving capability, both in number of long dives and duration of dives, with age (Lydersen et al. 1994), there was no evidence of bearded seal adults eating larger fish than pups in this study. Both pups and adults are benthic feeders and the sea floor is likely within reach of both age classes in our study area. Regardless, this improvement of diving capability with age supports the general effect of age on foraging capabilities between pups and adults of ice seals.

Fish lengths and weights estimated by OLFL relationships can be used to determine energy density of fishes eaten by ice seals. Fish length – fish weight relationships for 11 fish species commonly consumed by ice seals have recently been characterized in the Alaska Arctic (Chapter 1). With these relationships, and stomachs from the subsistence seal harvest, changes can be tracked in fish species eaten and the size distributions of those species as the Arctic environment changes. Otolith length – fish length relationships will allow studies of foraging flexibility and a better understanding of the potential resilience of ice seals to changes in diet by determining sizes of fish ice seals target during foraging. Fish size and location could be useful to identify important seal habitat and to study resource partitioning among seal species and age classes. Thus, determining sizes of fish consumed by ice seals in the Alaskan Arctic will aide biologists in a better understanding of ice seal feeding ecology and habitat use.

The four fish prey species consumed by the three seal species are considered to be high energy forage fishes in the Alaskan Arctic (Capelin, Arctic Cod, Saffron Cod, and Pacific Sand Lance). Capelin, Arctic Cod and Pacific Sand Lance have the highest mean wet mass energy density among the four species (Van Pelt et al. 1997, Harter et al. 2013). Pacific Sand Lance from the North Pacific can have a mean energy content of 5.31 kJ gr^{-1} wet mass (Van Pelt et al. 1997); Capelin from the North Pacific averaged 4.11 kJ gr^{-1} wet mass (Van Pelt et al. 1997); and Arctic Cod from the Beaufort Sea averaged 3.9 ± 0.21 kJ gr^{-1} wet mass (Harter et al. 2013). Another fish species present in the Chukchi Sea commonly consumed by ice seals, Walleye Pollock (*Gadus chalcogrammus*), has an energy density of 2.73 ± 0.26 kJ gr^{-1} wet mass (Van Pelt et al. 1997). The diet overlap among seal species in high energy content fish may have implications for species competition and provide insight into habitat partitioning among seal species. Using the average wet energy density of Arctic Cod, one Arctic Cod of the size and weight consumed by bearded seals (19.03 g - 153.85 g, Table 2.1) would contribute 4.88 - 39.45 kJ to their daily diet. Ringed seals consumed Arctic Cod weighing 7.28 g to 155.83 g (Table 2.1) that would contribute 1.87 to 39.95 kJ. Spotted seals consumed Arctic Cod that were larger (15.18 g to 172.45 g, Table 2.1) and would contribute 3.91 – 44.22 kJ to their daily diet. To extend the estimation of energy value in fishes commonly consumed by ice seals, energetic values are needed for more Alaskan Arctic fish species that are commonly consumed; i.e., Saffron Cod, Arctic Staghorn Sculpin, Shorthorn Sculpin, Slender Eelblenny, Stout Eelblenny, Canadian Eelpout, Yellowfin Sole and Bering Flounder.

Climate change will affect the Arctic ecosystem. A longer open water season will likely change fish species diversity and size distributions and, in turn, may influence ice seal distribution. For example, if fish shift the boundaries of their ranges northward in response to warming temperatures (Mueter and Litzow 2008), concurrent changes in the growth rates and size distribution of these fishes (Perry et al. 2005) may have important consequences for foraging ice seals. By understanding how ice seals are foraging now, scientists will be able to better predict how ice seal diets may change in the coming years.

Figures

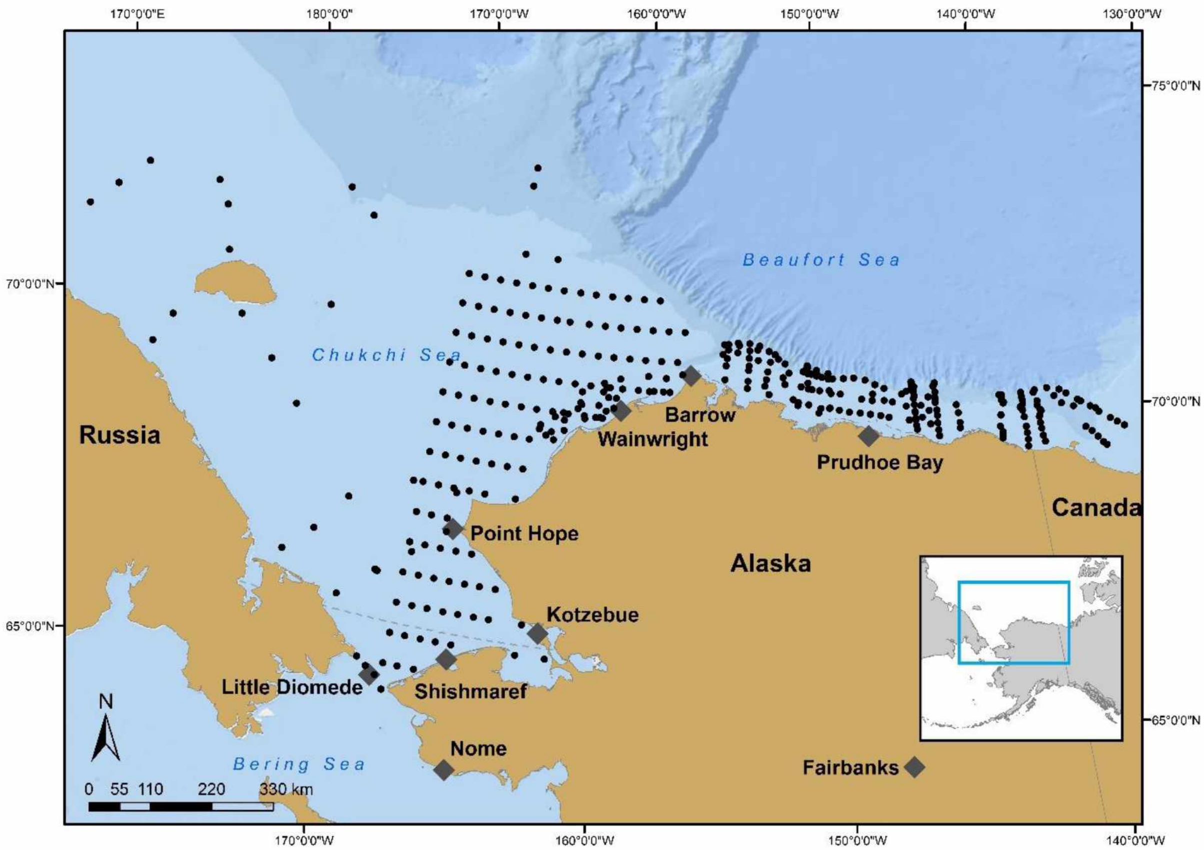

Figure 2.1. Study area. Diamonds (except for Prudhoe Bay and Fairbanks) indicate seal harvest location, black dots indicate fish sampling locations used to establish otolith length – fish length relationships (Chapter 1).

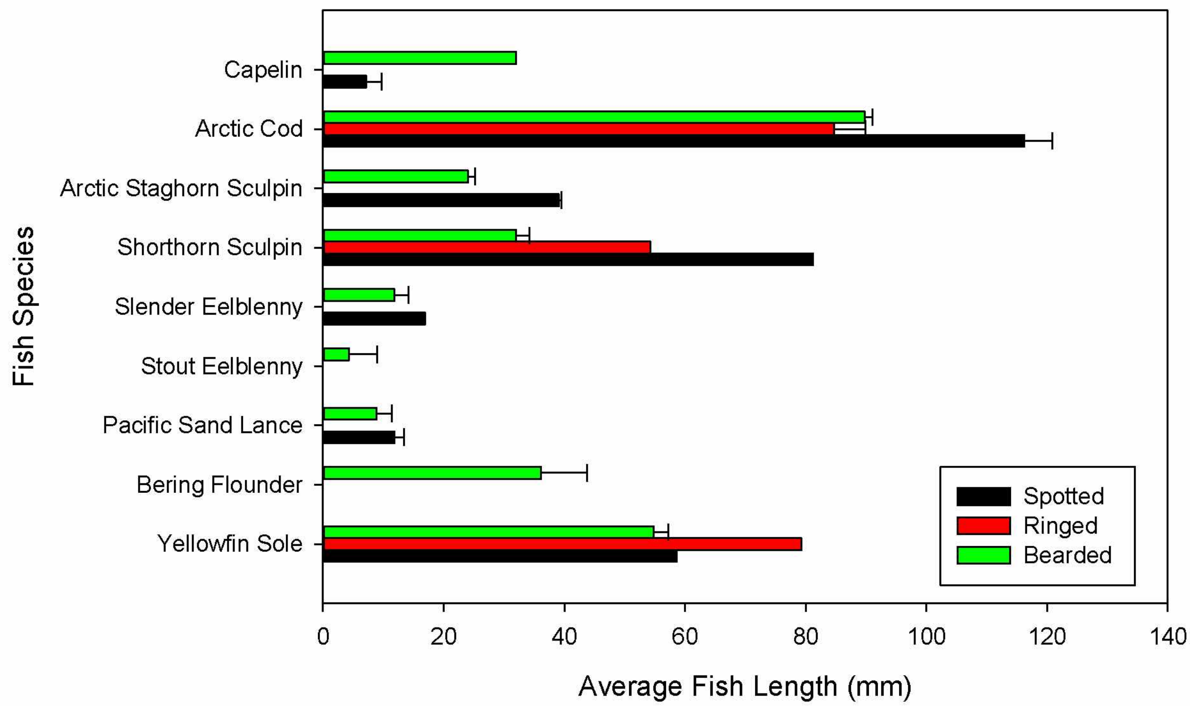

Figure 2.2. Average (± standard error) fish length (mm) of species consumed by three seal species (bearded, spotted and ringed seals) that had otolith lengths within the range of the otoliths used to develop the existing linear otolith length – fish length relationships. This figure does not include larger fish of these species or any Saffron Cod and Canadian Eelpout, which were also eaten by seals.

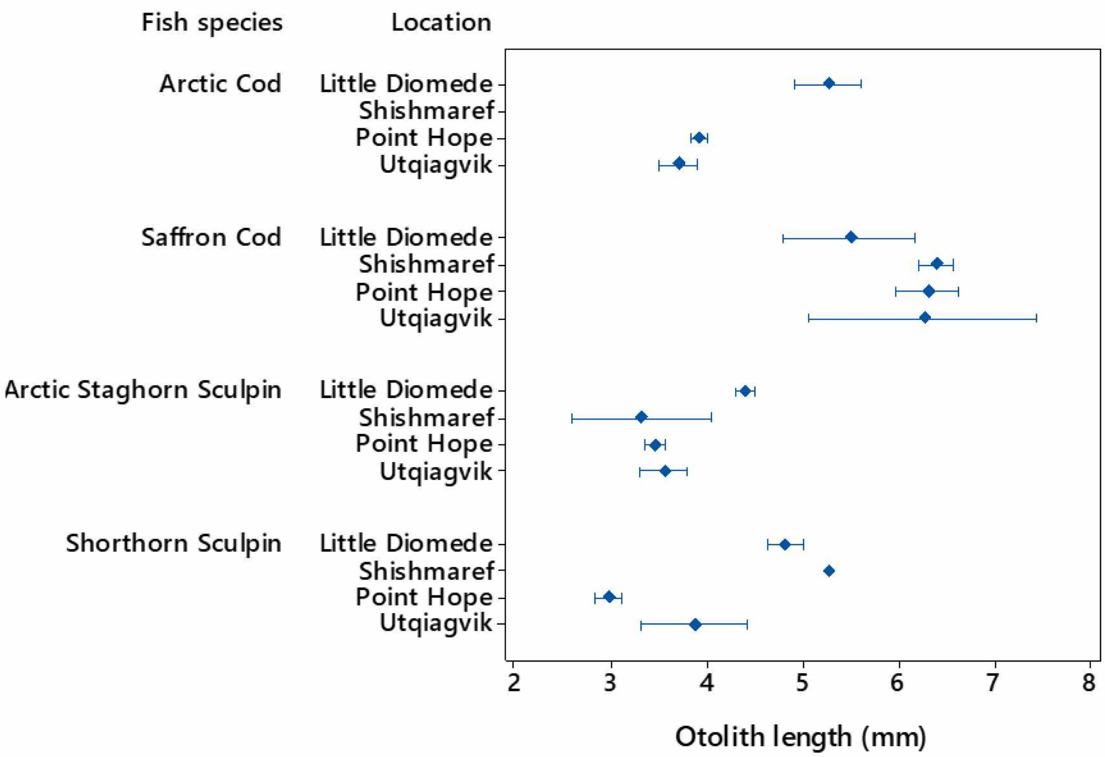

Figure 2.3. Interval plot of significant differences in otolith length among harvest locations for bearded seals. The distance between points indicates differences (non-overlapping error bars) in otolith length among harvest locations.

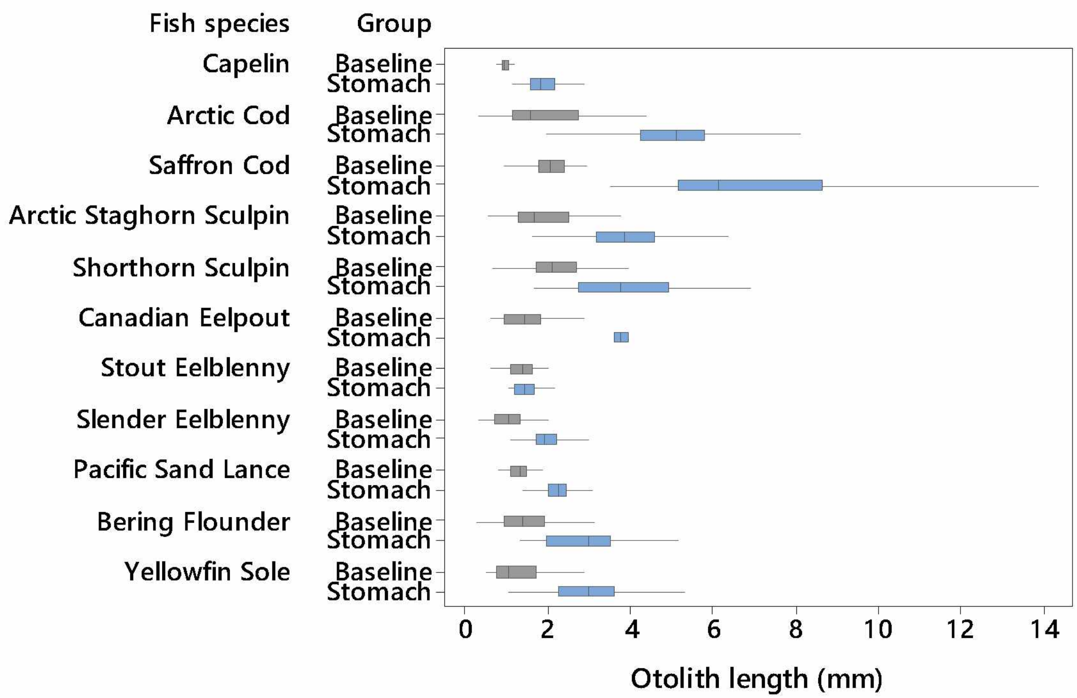

Figure 2.4. Box plot of otolith lengths (mm) of fishes consumed by ice seals (blue boxes, labeled as "Stomach") vs fishes in Chapter 1 use to create otolith length - fish length relationships (grey boxes, labeled as "Baseline"). Box plot includes median line, interquartile range box and whiskers that encompass more than 95% of data points. No outliers are shown.

Tables

Table 2.1. Average fish lengths (mm) and weights (g) of fish species consumed by Alaskan Arctic three seal species. The number of otoliths (n) used for length estimation is included.

	n	Average Fish Length	Minimum Fish Length	Maximum Fish Length	Average Fish Weight	Minimum Fish Weight	Maximum Fish Weight
Bearded Seal							
Capelin	1	110	110	110	6.28	6.28	6.28
Arctic Cod	242	229	143	284	85.14	19.03	153.85
Arctic Staghorn Sculpin	221	116	64	143	24.02	3.01	44.87
Shorthorn Sculpin	150	128	74	181	32.02	4.94	83.35
Slender Eelblenny	81	163	109	195	11.82	3.99	18.08
Stout Eelblenny	23	108	78	155	4.28	1.47	10.78
Pacific Sand Lance	21	142	112	159	8.89	3.82	12.92
Bering Flounder	31	146	83	202	36.12	4.32	79.53
Yellowfin Sole	161	150	59	200	54.77	2.27	119.92
Spotted Seal							
Capelin	2	113	109	118	7.08	6.03	8.14
Arctic Cod	99	242	129	285	116.18	15.23	172.45
Arctic Staghorn Sculpin	2	137	132	142	39.06	34.27	43.86
Shorthorn Sculpin	1	179	179	179	81.24	81.24	81.24
Slender Eelblenny	1	190	190	190	16.87	16.87	16.87
Pacific Sand Lance	8	155	136	161	11.81	7.44	13.36
Yellowfin Sole	1	160	160	160	58.60	58.60	58.60
Ringed Seal							
Arctic Cod	331	214	104	285	73.05	7.28	155.83
Shorthorn Sculpin	1	158	158	158	54.24	54.24	54.24
Yellowfin Sole	1	176	176	176	79.28	79.28	79.28

Table 2.2. ANOVA results for each seal species with significant results ($p < 0.001$) denoted by *.

Bearded

	Sum Sq	Mean Sq	DF	F.value	Pr(>F)
Location	41.309	13.7696	3	14.1511	7.03e-8*
Age Class	4.329	2.1646	2	2.2246	0.1127
Sex	5.093	2.5467	2	2.6172	0.0768

Spotted

	Sum Sq	Mean Sq	DF	F.value	Pr(>F)
Location	24.1102	24.1102	1	16.6509	0.0001*
Age Class	3.0004	1.5002	2	1.0361	0.3611
Sex	1.7071	0.8535	2	0.5895	0.5578

Ringed

	Sum Sq	Mean Sq	DF	F.value	Pr(>F)
Location	16.22	16.22	1	18.6924	3.15e-5*
Age Class	11.5777	5.7888	2	6.6712	0.002*
Sex	3.3978	1.6989	2	1.9579	0.1456

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General Conclusions

Otolith length – fish length (OLFL) relationships are known to be species specific, but they may also be regionally specific within species, necessitating caution in widespread applications. Fish growth varies by environmental conditions, including temperature, salinity and food supply, which account for regional differences in OLFL relationships (Mosegaard et al. 1988). For example, Arctic Cod (*Boreogadus saida*) found in the northern Bering and southern Chukchi seas are larger than their counterparts in the northern Chukchi Sea (Helser et al. 2015). If the Bering Sea has an environment more conducive for fishes such as Arctic Cod to grow larger than their counterparts, it is very likely that their OLFL relationships will differ among these three regions.

OLFL relationships were developed for 11 common Arctic fish species to further diet studies of marine piscivores in the Alaskan Arctic. A limitation of these study was that despite the generally linear relationship between otolith length and fish length, the relationship may change slightly for much smaller or much larger otoliths than those used for creating the linear function. In other words, the size range of fishes used to develop the original OLFL relationship may not be representative of the entire fish population or of the fraction of the fish population commonly consumed by ice seals or other predators. Using a larger range of fish otolith sizes than was available here to create more extensive OLFL relationships in future studies could result in a larger number of otoliths from seal stomachs to which size analyses could be applied. In addition, OLFL relationships only accurately apply to undamaged otoliths. Otoliths erode once exposed to digestive acids in a predator's stomach, making it imperative that OLFL relationships only be applied to otoliths that retained their species-specific shape. This risk is generally reduced because of the relatively short time (12 to 24 hours; Murie and Lavigne 1986) that otoliths remain in seal stomachs. Eroded otoliths will not produce accurate length estimates compared with fresh and undamaged otoliths, however they will always be biased low and could provide a minimum size of fish eaten, which may be acceptable in some studies. Despite these limitations, OLFL relationships are still vital in furthering piscivore diet studies and are key in future energetics studies of piscivorous marine mammals in the Arctic.

Although bearded, spotted, and ringed seals generally differed in the fish composition of their diet, all three species consumed Capelin (*Mallotus villosus*), Arctic Cod, Saffron Cod (*Eleginus gracilis*), and Pacific Sand Lance (*Ammodytes hexapterus*). These four fish species are very high in energy content (Van Pelt et al. 1997, Harter et al. 2013), likely making them highly valuable prey for seals. It is possible that some of these differences and similarities in diets among the three seal species are influenced by their foraging locations. Seals that were harvested in more southern locations (Shishmaref and Little Diomede) consumed larger fish of the same species than seals harvested in northern locations (Utqiagvik and Point Hope), likely reflecting differences in the fish size structure in these different locations. Future shifts in fish populations or seal foraging locations thus could influence prey size availability to seals. Intraspecific competition may be modulated by different fish size preferences by seal age. Older seals within a species generally consumed larger fishes than younger seals, likely driven by physiological diving and foraging constraints for pups (Noren et al. 2005). Size separation, however, provides effective resource partitioning and reduction of competition between adult seals and their offspring. The overlap in prey species for all three seal species could lead to interspecific competition of prey resources. There was a trend, although not statistically significant, that different seal species consumed different sized Arctic Cod, possibly reducing competition among species for this key link in the Arctic marine food web (Hop and Gjøsæter 2013).

These relationships provide an essential stepping stone for the investigation of bioenergetics of seal and other top fish predators. Building on this prey fish size information from the OLFL relationships, energetic value of the prey can be calculated from known fish size-biomass relationships and energetic values per fish biomass. Thus, applying OLFL to otoliths from seal stomachs, biologists will be able to determine the energetic importance of various fish species to an ice seal's or other piscivore's diet. These results provide an important basis to evaluate ramifications of possible changes in fish distributions or size structure based on the ongoing environmental changes in the Arctic (Perry et al. 2005). Similarly, there may be changes in seal foraging behavior that may result in different use of fish prey (Moore and Huntington 2008, Kovacs et al. 2011).

The Alaskan Arctic is just one of many environments being affected by climate change. The results of this study will help biologists better understand the predator-prey relationships of ice seals and fishes. If climate change affects the distribution and size structure of important fish species, it will simultaneously affect the distribution and/or the diet of ice seals. As a next step, it would be useful to determine energetic values by region of the fish prey of ice seals so that energetic values of prey species can be assessed for important top predators of the Arctic marine ecosystem. Developing a better knowledge base about ice seals and their fish diet preferences is essential to determining the future of these species in the Arctic.

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